A COMMENTARY ON RECENT CHANGES TO BUTTERFLY DISTRIBUTIONS IN THE LONDON AREA

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Abstract

Changes in the distribution of butterfly species are presented from the London area for the period 1980-2000. Most species (65%) became more widespread, including some habitat specialist butterflies, but a few show substantial declines in distribution. Although incomplete data prevent a systematic assessment of the biasing effects of recording effort variation, other data are presented (e.g. from abundance monitoring, national distribution trends and site colonisations) to suggest that the distribution changes are genuine. Some of the possible causes of these patterns are discussed.

Introduction

Much recent attention has been focussed on changes in the distribution of species, particularly in response to climate change and habitat loss. Studies have identified patterns of range change amongst different taxa that are consistent with a climate explanation at global (e.g. Parmesan and Yohe 2003, Root *et al.* 2003), European (e.g. Parmesan *et al.* 1999) and British (e.g. Thomas and Lennon 1999, Warren *et al.* 2001, Hickling *et al.* 2005) scales. Such studies have sought evidence from distribution survey data for changes in species range occurring at latitudinal and altitudinal margins. Amongst British butterflies, northward extensions of range margins (although not range shifts) have been identified for 11 species (c. 25% of the southerly distributed species) and some evidence found for a shift to higher altitude amongst species with northern and/or montane distributions (Hill *et al.* 2002).

Habitat loss, fragmentation and degradation and their effects on the distribution of butterflies in Britain have been widely documented (e.g. Heath *et al.* 1984, Warren 1992, Fox 2001, Asher *et al.* 2001) and these should be considered in the context of spatially realistic metapopulation theory (Ehrlich and Hanski 2004). Some butterfly studies have looked at the important interaction between climate suitability and the availability, spatial distribution and quality of habitat in determining species responses (e.g. Hill *et al.* 1999, Thomas *et al.* 1999, Hill *et al.* 2001, Thomas *et al.* 2001, Warren *et al.* 2001), but these have focussed on large geographical areas and/or networks of conservation priority habitats such as unimproved calcareous grassland and lowland heath. Patterns of distribution change other than at latitudinal or altitudinal margins, and in urban landscapes have rarely been considered (but see Hardy and Dennis 1999, Dennis and Hardy 2001). Here we present an analysis of recent distribution change across the butterfly fauna of a major urban area; London, UK.

Methods

Study area

For the purposes of this study, the London area is defined as the recording area of the London Natural History Society (LNHS). This was originally a 20-mile radius from St Paul's Cathedral, but the current boundary is a stepped polygon, incorporating only complete 2km square divisions of the Ordnance Survey National Grid. The area consists of 856 2km squares, equivalent to 3424 km². From the centre outwards this encompasses central London, inner-city urban areas, substantial areas of suburbia and then a range of agricultural and semi-natural areas with significant human habitation and development.

Administratively the study area includes Greater London (made up of the 32 London Boroughs and the City of London) and adjacent parts of the counties of Hertfordshire, Essex, Kent, Surrey and Buckinghamshire. Together these fringing areas make up a substantial portion of the total study area, as well as containing a disproportionate amount of semi-natural habitats important to specialist butterflies (e.g. chalk grassland).

Greater London (at the core of the study area) includes less semi-natural habitat, although it contains a high proportion of greenspace. Gardens and parks make the greatest contribution to this greenspace, with approximately 31,600 ha of private gardens (c. 20% surface area) and approximately 21,000 ha of parks and amenity grassland (c. 13% surface area), but Greater London retains important areas of woodland and neutral grassland, as well as smaller areas of other semi-natural habitats (London Biodiversity Partnership www.lbp.org.uk).

Distribution data sources and date classes

The butterflies of the London area have been comprehensively surveyed in two recent periods. A Butterfly Atlas project organised by LNHS gave rise to distribution maps (at $2\text{km} \times 2\text{km}$ grid square resolution) based on the 1980-1986 period (Plant 1987). Less than a decade later, the Butterflies for the New Millennium (BNM) project was launched to record butterfly distributions across the whole of Britain and Ireland. Data from the first 5-years of recording (1995-1999) for the BNM project were used to produce a new Britain and Ireland atlas (Asher *et al.* 2001). Although this atlas presented distributions at a 10km grid square scale, over 93% of the records in the extensive data set collated by the ongoing BNM project have a spatial resolution of 100m or 1km.

In common with most distribution recording schemes, both these data sets were collated from *ad hoc* observations. Such an approach is a traditional and practical way to collect distribution records, which then inform many biodiversity conservation programmes. However, collations of *ad hoc* records contain substantial temporal, spatial and taxonomic biases that are difficult to quantify and remove from distribution data sets (Dennis and Thomas 2000, Asher *et al.* 2001, Dennis *et al.* in press). It is essential to consider such bias when comparing species distribution in two date periods. Recording coverage is perhaps the most important element of such

bias. Complete recording coverage of 2km squares in the study area was achieved by the 1980-86 London survey. However, the presence of at least one species in every grid square does not prove that the survey recorded all butterfly species present in each square. Complete coverage was not achieved in the subsequent survey period, but recording may have been more thorough within the visited squares.

It was important to try to match the level of recording coverage as closely as possible between the two date classes in which butterfly distributions were to be compared. The baseline survey spanned a seven year period, but since, the intensity of biological recording across a wide variety of taxa has tended to increase in Britain during recent years, it was not necessarily fair to compare this baseline with an equivalent seven year date class from the BNM data set. Unfortunately, the raw data from 1980-86 was not available so detailed assessment of coverage (e.g. number of visits to each grid square) was impossible. In the absence of such information, a rough estimate of coverage was used to determine the most appropriate length of the second date class. The average number of occupied 2km squares for the six butterfly species expected to have a ubiquitous distribution in the study area was taken for the 1980-86 period and compared to the averages generated from BNM maps based on 1995-99, 1995-2000 and 1995-2001 date periods (i.e. 5, 6 and 7 year surveys). The 1995-2000 period achieved the closest match using this simple technique and so was used for the assessment.

Assessing species distribution

Butterfly distributions in the London area were calculated for all resident species as the number of occupied 2km squares. As previously noted, the data used to prepare the maps in the London atlas (Plant 1987) were not available so distributions were assessed by counting the dots (occupied 2km squares) on each species map. The BNM database was used to plot 2km distribution maps for the same species over the 1995-2000 period. The mapping programme calculated the number of occupied squares for each species automatically.

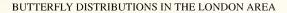
Proportional distribution change was calculated as the difference in the number of occupied 2km squares between the two date periods, divided by the number of occupied squares in 1980-86.

Results

Two thirds of resident species (26/40 species) increased in distribution in the London area between the 1980-86 and 1995-00 surveys (Table 1, Figure 1). In addition, four species (all very rare) remained stable over the period, meaning that a quarter of species (10/40) declined. Note that for some species the number of occupied squares was numerically low, particularly for some butterflies that only occur at the edge of the LNHS recording area, and measures of change for these could be affected by sampling errors.

| Species | | 1980-1986 occupied squares | 1995-2000 occupied squares | Proportional distribution change % |
|---------------------------|------------------------|----------------------------------|----------------------------------|--|
| Small Skipper | Thymelicus sylvestris | 636 | 603 | -5 |
| Essex Skipper | Thymelicus lineola | 570 | 567 | -1 |
| Silver-spotted Skipper | Hesperia comma | 5 | 11 | 120 |
| Large Skipper | Ochlodes sylvanus | 614 | 540 | -12 |
| Dingy Skipper | Erynnis tages | 33 | 44 | 33 |
| Grizzled Skipper | Pyrgus malvae | 35 | 53 | 51 |
| Brimstone | Gonepteryx rhamni | 402 | 520 | 29 |
| Large White | Pieris brassicae | 710 | 757 | 7 |
| Small White | Pieris rapae | 828 | 765 | -8 |
| Green-veined White | Pieris napi | 719 | 759 | 6 |
| Orange-tip | Anthocharis cardamines | 500 | 656 | 31 |
| Green Hairstreak | Callophrys rubi | 33 | 59 | 79 |
| Brown Hairstreak | Thecla betulae | 4 | 4 | 0 |
| Purple Hairstreak | Neozephyrus quercus | 124 | 396 | 219 |
| White-letter Hairstreak | Satyrium w-album | 22 | 168 | 664 |
| Small Copper | Lycaena phlaeas | 355 | 445 | 25 |
| Small Blue | Cupido minimus | 17 | 21 | 24 |
| Silver-studded Blue | Plebeius argus | 2 | 2 | 0 |
| Brown Argus | Aricia agestis | 21 | 237 | 1029 |
| Common Blue | Polyommatus icarus | 587 | 573 | -2 |
| Chalkhill Blue | Polyommatus coridon | 15 | 30 | 100 |
| Adonis Blue | Polyommatus bellargus | 2 | 3 | 50 |
| Holly Blue | Celastrina argiolus | 330 | 687 | 108 |
| Duke of Burgundy | Hamearis lucina | 4 | 1 | -75 |
| White Admiral | Limenitis camilla | 49 | 85 | 73 |
| Purple Emperor | Apatura iris | 8 | 21 | 163 |
| Small Tortoiseshell | Aglais urticae | 856 | 749 | -13 |
| Peacock | Inachis io | 678 | 759 | 12 |
| Comma | Polygonia c-album | 590 | 680 | 15 |
| Pearl-bordered Fritillary | Boloria euphrosyne | 2 | 2 | 0 |
| Dark Green Fritillary | Argynnis aglaja | 12 | 35 | 192 |
| Silver-washed Fritillary | Argynnis paphia | 13 | 53 | 308 |
| Speckled Wood | Pararge aegeria | 395 | 708 | 79 |
| Wall | Lasiommata megera | 354 | 63 | -82 |
| Marbled White | Melanargia galathea | 20 | 121 | 505 |
| Grayling | Hipparchia semele | 3 | 3 | 0 |
| Gatekeeper | Pyronia tithonus | 521 | 701 | 35 |
| Meadow Brown | Maniola jurtina | 768 | 743 | -3 |
| Ringlet | Aphantopus hyperantus | 121 | 265 | 119 |
| Small Heath | Coenonympha pamphilus | 442 | 295 | -33 |

Table 1. Distribution change of butterflies in the London area between 1980-86 and 1995-2000.



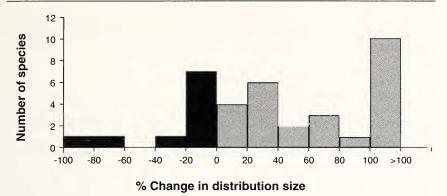


Figure 1. Proportional distribution changes of butterflies in the London area between 1980-86 and 1995-2000.

These results suggest that the distribution of 10 species more than doubled (in terms of the total number of 2km squares) in the London area, and a greater than threefold increase in occupied squares was recorded for five of these. The greatest increase recorded was for the Brown Argus *Aricia agestis*, which was observed in only 21 2km squares in the 1980-86 survey. By the 1995-00 survey, this species was found to occupy 237 2km squares, a proportional increase of 1029% (Figure 2). Other species exceeding a 200% increase in distribution are the White-letter Hairstreak *Satyrium w-album*, Marbled White *Melanargia galathea*, Silver-washed Fritillary *Argynnis paphia* and Purple Hairstreak *Neozephyrus quercus*.

Habitat specialist butterflies appear to have fared well. The calcareous grassland species Silver-spotted Skipper *Hesperia comma*, Chalkhill Blue *Polyommatus coridon* and Dark Green Fritillary *Argynnis aglaja* all increased by at least 100% and the results are also positive for some woodland specialists such as Silver-washed Fritillary, Purple Emperor *Apatura iris* and White Admiral *Limenitis camilla*.

Generalist butterflies such as the Holly Blue *Celastrina argiolus* and Speckled Wood *Pararge aegeria* (Figure 3) show the greatest increases in the number of occupied 2km squares (as opposed to proportional increase).

Most of the species that show a decrease in the number of recorded 2km squares between the two surveys are common, generalist species and their declines are negligible (e.g. c.10% decrease). Such species, the Common Blue *Polyommatus icarus*, Small White *Pieris rapae*, Small Tortoiseshell *Aglais urticae* and Meadow Brown *Maniola jurtina* are amongst the most widespread species in the London area and across Britain.

The results for three species do give greater cause for concern however. One rare, specialist species, the Duke of Burgundy *Hamearis lucina* appears to have been lost from three of the four 2km squares occupied during the 1980-86 survey on the southwestern edge of the recording area, which forms part of the limited range of this species in Surrey (Collins 1995).

In addition, the recorded distributions of two once regionally widespread species decreased substantially; the Wall *Lasionmata megera* by 82% (Figure 4) and the Small Heath *Coenonympha pamphilus* by 33% (Figure 5).

Discussion

This study shows that more butterfly species (65%) extended their distribution in the London area than declined during the 1980s and 1990s. This is in contrast to comparable national scale assessments. Warren *et al.* (2001) found that three quarters of non-migratory butterflies had declined in distribution in Britain between the 1970s and 1995-99. The discrepancy is explained, at least in part, by the fact that some of the most rapidly declining species nationally were extinct in the London area prior to the 1980-86 survey (e.g. the Wood White *Leptidea sinapis*, Small Pearlbordered Fritillary *Boloria selene*, High Brown Fritillary *Argynnis adippe* and Marsh Fritillary *Euphydryas aurinia*).

Sampling effort

Without access to and computerisation of the full set of 1980-86 survey butterfly records it is impossible to measure any effects caused by variation in sampling effort between the two survey periods and this has hindered the application of any analytical procedures to the data. Our approach is to present the recorded change in distribution for each species and provide other evidence (e.g. from transect data).

However, some general comments can be made with regard to sampling effort. First, the overall coverage in the first survey period was better than in 1995-2000. At least one species was recorded from every 2km square in 1980-86. Second, the duration of the later survey period was selected so as to provide a similar level of coverage for the most widespread species. Third, the fact that both substantial decreases and increases in distribution have been revealed in this study suggests that these are real biogeographic patterns and not the result of a sampling artefact. Finally, there are general similarities between species distribution changes and abundance changes in London, as well as with distribution changes across Britain.

Therefore, whilst we are confident that sampling effort has not been a major influence on our study overall, we cannot assess the potential biasing effects on individual species. Species that are less apparent (because of behaviour, size, colour, flight period, biotope use or population density) to recorders are likely to be recorded only after repeated visits to a square (Dennis *et al.* in press). The number of recording visits made to a grid square has been shown to significantly influence both the total number of recorded species and the probability of recording each individual species in butterfly surveys of Greater Manchester (Dennis *et al.* 1999, Dennis and Hardy 1999). We suspect that the canopy dwelling species Purple Hairstreak, White-letter Hairstreak and Purple Emperor are more likely to have been under-recorded in squares that have received a low number of recording visits.

Comparison with abundance data from butterfly transects

The distribution changes of London's butterflies reported here can be compared with abundance data collated from transect monitoring that takes place at sites across Greater London following the standard methodology used in the UK Butterfly Monitoring Scheme (Pollard and Yates 1993). Although the first transect in the Greater London area (at Hampstead Heath) has been running continuously since 1978, many London transects have been established only recently. By 2000, data could be drawn from 19 transects, but many of these had only short time series of data (e.g. 10 sites only joined the scheme during 1999!) (Williams 2000). However, collated indices of butterfly abundance in Greater London have been calculated for all generalist species since 1990 and several habitat specialist species have been added since 1997 (Williams 2002). It must be recognised that these collated indices only represent Greater London, not the whole study area. Furthermore, an assessment of the data gathered up to 2000 concluded that few species showed a significant trend in abundance, probably because the large fluctuations in population levels typical of butterflies act to obscure long-term trends in short time series data (Williams 2001). This problem will be alleviated as further years of transect data are added in the future. Nevertheless, the index values for London's butterflies do represent the core part of the study area where many of the most dramatic distribution changes have taken place and can be informative even without statistical tests of trend significance.

Some of the species that have the most rapidly expanding distributions in the London area are generally not well covered by local transect monitoring, either because they are canopy species not well suited to the sampling method (e.g. Purple Hairstreak and White-letter Hairstreak) or because they occur at too few monitored sites to derive a reliable population index (e.g. Dark Green Fritillary and Silver-washed Fritillary). However, other rapidly expanding species show clear increases in index values since monitoring began. Population index values for the Ringlet *Aphantopus hyperantus* (which showed a distribution increase of 119%) have been above the 1990 baseline level in every year since except one (1996). Speckled Wood (79% distribution increase) and Gatekeeper *Pyronia tithonus* (35% increase) both have index values above the baseline level in eight out of ten years.

Similarly, the rapid distribution declines of the Wall and Small Heath are corroborated by London transect indices. The Wall has become extinct on all transect routes within Greater London (last recorded in 1995) and the Small Heath's collated index has remained below the 1990 baseline index in every year. Its population level in 2000 was the second lowest in the series.

For a few species, the distribution and abundance data present opposite views. The Brown Argus is an example. It has undergone a massive distribution increase since the mid-1980s, but the London transect data suggest a decline between 1990 and 2000, albeit with large fluctuations from year to year. We might not expect the distribution and abundance data to corroborate one another for this species because much of the species distribution expansion has been in those parts of the study area outside of the Greater London boundary (e.g. in Hertfordshire to the north and Essex to the east, and also in Surrey and Kent to the south). Nevertheless it has been shown that species national distribution change and abundance change are highly significantly correlated (Warren *et al.* 2001). Furthermore, the Brown Argus' regional abundance indices for South-east England derived from the Butterfly Monitoring Scheme (David Roy pers. comm.) show increasing population levels in both generations (although this is statistically significant for the second generation only) and the species' national distribution has also increased substantially since the 1970s (Asher *et al.* 2001).

Possible explanations for this discrepancy are that the distribution increase may have happened during the late 1980s and early 1990s, but the butterfly may have declined since then, or that specific factors (most likely related to habitat) are leading to population decline at some or all of the monitored sites (only seven transects recorded this species in Greater London in 2000) whilst the species continues to do well elsewhere. Based on an index value of 100 in 1990, the species' transect index for Greater London increased to 136 in 1991, had declined to 18 in 1993, was back at 100 in 1995, 11 in 1998; (and a low of seven in 2001 rising to 41 in 2004).

The typical habitat of the Brown Argus is calcareous grassland, though it also occurs on coastal grasslands, in woodland clearings, heathland, disused railway lines, road verges and on set-aside fields (Asher et al. 2001). The presence of all these habitats is limited in Greater London and many areas of non-calcareous rough grassland have been lost to scrub and woodland, or to built development. Comparison of regolith maps and of the distribution of the Brown Argus in London and the surrounding counties (e.g. see Burton 1983, Collins 1995, Sawford 1987, Murray and Wood 2001, and the comments in Asher et al. 2001) suggests that the presence of chalk habitats is a significant factor for the Brown Argus. The main increase in range and abundance has been in the countryside beyond Greater London, particularly in the vicinity of chalk grasslands. The species has increased its range on the chalk of the south of Greater London too, but has also colonised sites away from the chalk (e.g. Mitcham Common, Wimbledon Common and Richmond Park). Thus much of London particularly in the north-west is geologically unsuitable for the Brown Argus, whilst elsewhere in London the primary and secondary grassland habitats for this species are unavailable due to loss to built development or because of succession to woodland. The evidence suggests therefore that, due to a combination of geological and ecological factors, the Brown Argus behaves as a habitat specialist in Greater London but more typically as a wider countryside species in the areas surrounding Greater London.

Comparison with national distribution change

We can also interpret the distribution trends found in the London area with those found at the national level (Asher *et al.* 2001). In most cases species faring well in London have also done well at the national level since the 1970s, including the Orange-tip *Anthocharis cardamines*, Purple Hairstreak, Speckled Wood, Marbled

White, Gatekeeper and Ringlet. All of these generalist species are undergoing national range expansions. In addition, the London area increases in distribution of some habitat specialist butterflies such as the Silver-spotted Skipper, White Admiral and Silver-washed Fritillary are also reflected in national distribution data. National surveys of the Silver-spotted Skipper, a UK Biodiversity Action Plan Priority Species, were conducted in 1982 and 2000 (corresponding well with the London survey periods) and revealed a threefold increase in the number of occupied 2km squares and even larger increases in the number of populations and area of habitat occupied (Davies *et al.* 2005).

All three of the butterfly species with severely declining distributions in the London area (the Duke of Burgundy, Wall and Small Heath) have also decreased rapidly at the national level.

Whist many species show similar trends in London and nationally, this is not true for all species. In particular, national assessments point to strong declines for the Dingy Skipper *Erynnis tages*, Grizzled Skipper *Pyrgus malvae*, Pearlbordered Fritillary *Boloria euphrosyne* and Dark Green Fritillary. By contrast, some of these species increased in the LNHS recording area between 1980-86 and 1995-2000. Although the possibility of the discovery of previously unknown populations in London during the second survey cannot be completely discounted, a real increase in population distribution would appear a more likely explanation.

The apparent increase in the distribution of the Purple Emperor, a woodland specialist, in the London area was almost entirely in the wider LNHS area beyond the Greater London boundary and was probably due to more intensive recording. Recent targeted surveys for this species in Hertfordshire have 'discovered' the species in many places, where it has probably survived unnoticed for decades (Goodyear and Middleton 2003).

Drivers of change: climate and habitat

Aside from the potential artefact of changing recording effort, what environmental factors could be driving the changing distribution patterns reported here? As discussed in the introduction, habitat change and climate change have been identified as important drivers of distribution change in butterflies and other taxa in Britain and elsewhere.

At the national scale, climate change is thought to be the most important driver of range expansion for generalist butterfly species (Asher *et al.* 2001, Warren *et al.* 2001, Hill *et al.* 2002). However, at first inspection, the climatic conditions of the London area would appear to be well within the tolerance range of these species already and, indeed, their expanding range margins have occurred at much higher latitudes. The expansion of the Orange-tip over the past three decades has occurred mainly in southern and central Scotland, and those for the Gatekeeper and Ringlet have occurred in the Midlands of England and in Yorkshire. Nevertheless, a close examination of national expansion patterns shows that some generalist species have been extending their distributions in a north-easterly direction within South-east

England (e.g. from Surrey towards Essex). Our study reveals that the distribution change for species such as Marbled White and Ringlet, which were quite localized species in the 1980-86 survey, has been concentrated in the southern and western parts of the London area.

Local infilling of sites within the existing range of species may possibly be assisted by climate amelioration allowing lower quality habitat to be colonised. Similarly, if climate change is influencing population size, then more individuals may be available to disperse and to establish new local populations.

An increasingly favourable climate has been linked with the expansions of specialists such as the White Admiral and Silver-spotted Skipper. Silver-spotted Skipper colonies can now occupy cooler calcareous grassland sites (e.g. those with taller vegetation or non-southerly aspects) than they could in the early 1980s (Thomas *et al.* 2001) and this has increased the total amount of potential habitat available to the species. However, in both cases habitat change is likely to be a significant factor as well. For example, for the Silver-spotted Skipper, grazing as part of conservation management as well as by wild herbivores (particularly rabbits) has been a factor in the spread of this butterfly (Davies *et al.* 2005).

There is a pattern shown in the distribution changes that some of the generalist species have colonised the more central, urban parts of the London area from the fringes. The Gatekeeper shows this pattern of change particularly well, with much of the distribution increase between the two surveys occurring in inner London Boroughs (e.g. Lewisham, Southwark, Kensington & Chelsea, Hammersmith & Fulham) and new locations being recorded at places such as Buckingham Palace garden, the Tower of London, Finsbury Park, New Cross Gate, Russia Dock, Holland Park, the Natural History Museum garden in Kensington, and Barnes Common (Figure 6). Transect data have also indicated a large increase in the abundance of the Gatekeeper in Greater London.

The Purple Hairstreak is another example. Although it is a canopy species and, therefore, one that can go unnoticed by recorders, there appears to have been an expansion across London and into the inner city area (e.g. in the Boroughs of Kensington and Chelsea, Lambeth, Lewisham, Southwark and Wandsworth). The species has recently been observed at localities such as Holland Park, Streatham Common, Wandsworth Common and Tooting Common. Of course, improved recording can never be ruled out and we would welcome any records from these sites that might indicate a longer history of occupancy by these species.

Unfortunately, there are no data on the changing extent (or quality) of habitats in this central urban area or across London as a whole (Dave Dawson pers. comm.). However, there are some trends in London that may have influenced the changing distributions of butterflies. Wood and Pullin (2002) suggested that four species of generalist butterfly in Birmingham were limited by availability of habitat and had sufficient dispersal ability to colonise suitable patches within the urban landscape. In London, there has been a substantial shift in the way that many public open spaces (and even transport corridors) are managed since the early 1980s. Many public open spaces now have at least one area that is left to 'go wild' during the summer, rather

than being mowed short throughout the growing season. These new areas of tall grassland have presented opportunities for colonization and increase for some grassland butterflies, particularly the Gatekeeper and Ringlet. Increasing awareness of nature conservation, together with wildlife gardening and the declaration of Local Nature Reserves, may have contributed, at least in part, to the recent successes of some of London's butterfly species.

Despite these improvements, over the same period there has been a significant loss of early-successional open habitats, both to urban development and to scrub and woodland. Butterflies such as the Wall and Small Heath are associated with areas of short, open grassland where there are patches of bare or stony ground. In our study area, brownfield sites, 'wasteland' and the margins of transport corridors are particularly important for such habitat conditions. The loss of London's wastelands has reduced the available habitat for these heat-loving butterflies and may be responsible, at least in part, for their distribution decline. No figures are available for this loss of habitat, but the London Biodiversity Partnership states: "Whatever the true extent of London's urban wasteland resource in the mid-1980s, there is no doubt that there has been a substantial reduction in its extent within the last decade. London's former docklands contained a significant proportion of the capital's urban wastelands, but most of this area has been redeveloped to accommodate London's burgeoning service sector industries. Other large areas have been lost in more recent years to provide land for new housing." (London Biodiversity Partnership, www.lbp.org.uk).

Aside from destruction of early-successional habitats, more insidious processes (e.g. eutrophication) may also be exerting significant influence. Analysis of terrestrial plant communities has shown increases of species that can tolerate high soil nutrient levels and decreases for those that cannot (Haines-Young *et al.* 2000, Preston *et al.* 2002). Pollard *et al.* (1998) identified eutrophication as one of the likely causes of a great increase in cover of coarse grasses at Monks Wood in Cambridgeshire, which they linked to increased abundance of butterfly species that use these grasses as larval hostplants (e.g. Large Skipper *Ochlodes sylvanus*, Speckled Wood and Ringlet). The spread of coarse grasses and other tall plants at the expense of finer grasses and shorter vegetation could be linked to the decline of species such as the Small Heath and Wall. The longer growing season made possible by climate change may also be exacerbating nutrient enrichment and contributing the decrease in broken turf micro-habitats that are so important to these butterfly species.

Conclusions

Clear changes have taken place to the distribution of butterflies in the London area in recent decades. Many species have increased, colonising new sites and spreading into more urban parts of London. However, although we believe this to be a biogeographical pattern, rather than an artefact of increased recording effort, we don't yet understand the causes. Climate change is known to be affecting the distributions of butterflies, both generalists and habitat specialists, at the national

scale, and it seems likely that there will be some local effects in the London area too. Another factor is that many of London's parks, cemeteries, gardens and open spaces are being managed in an increasingly wildlife-friendly way. However, other habitats have been lost during the same period, particularly with redevelopment of brownfield or 'wasteland' habitats, which are important for butterflies and a wide range of other invertebrate species.

Acknowledgements

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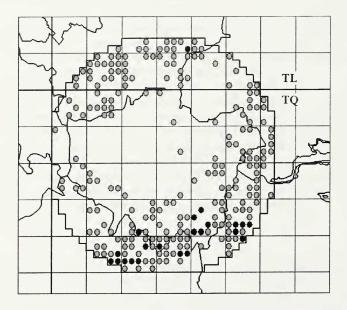


Figure 2. Distribution of the Brown Argus showing a 1029% increase in occupied 2km squares between survey periods. Black dots= occupied 1980-86, grey dots= occupied 1995-2000 only.

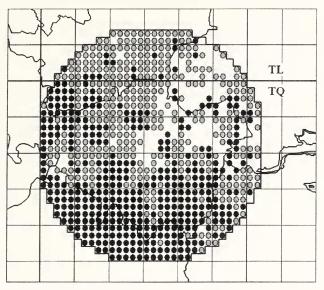


Figure 3. Distribution of the Speckled Wood showing a 79% increase in occupied 2km squares between survey periods. Black dots= occupied 1980-86, grey dots= occupied 1995-2000 only.

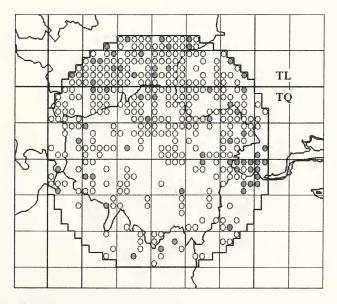


Figure 4. Distribution of the Wall showing an 82% loss of occupied 2km squares between survey periods. Open dots= last occupied 1980-86, grey dots= occupied 1995-2000.

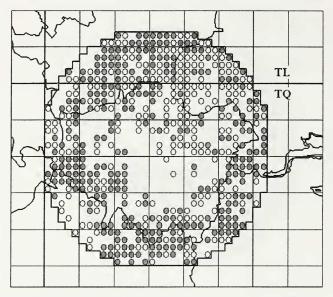


Figure 5. Distribution of the Small Heath showing a 33% loss of occupied 2km squares between survey periods. Open dots= last occupied 1980-86, grey dots= occupied 1995-2000.

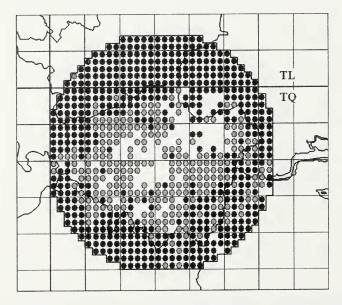


Figure 6. Distribution of the Gatekeeper showing a 35% increase in occupied 2km squares between survey periods. Black dots= occupied 1980-86, grey dots= occupied 1995-2000 only.

References

- Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G. and Jeffcoate, S., 2001. *The millennium atlas of butterflies in Britain and Ireland*. Oxford University Press, Oxford.
- Burton, R. M. 1983., Flora of the London area. London Natural History Society, London.
- Collins, G. A., 1995. Butterflies of Surrey. Surrey Wildlife Trust, Pirbright.
- Davies, Z. G., Wilson, R. J., Brereton, T. M. and Thomas, C. D., 2005. The re-expansion and improving status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain: a metapopulation success story. *Biological Conservation* 124: 189-198.
- Dennis, R. L. H. and Hardy, P. B., 1999. Targeting squares for survey: predicting species richness and incidence of species for a butterfly atlas. *Global Ecology and Biogeography Letters* 8: 443-454.
- Dennis, R. L. H. and Thomas, C. D. 2000. Bias in butterfly distribution maps: the influence of hot spots and recorder's home range. *Journal of Insect Conservation* 4: 73-77.
- Dennis, R. L. H. and Hardy. P. B., 2001. Loss rates of butterfly species within urban development. A test of atlas data and sampling artefacts at a fine scale. *Biodiversity and Conservation* **10**: 1831-1837.
- Dennis, R. L. H., Sparks, T. H., and Hardy, P. B., 1999. Bias in butterfly distribution maps: the effects of sampling effort. *Journal of Insect Conservation* **3**: 33–42.
- Dennis, R. L. H., Shreeve, T. G., Isaac, N. J. B., Roy, D. B., Hardy, P. B., Fox, R. and Asher, J., (in press). The effects of visual apparency on bias in butterfly recording and monitoring. *Biological Conservation*.
- Ehrlich, P. H. and Hanski, I., 2004. On the wings of checkerspots. Oxford University Press, New York.
- Fox, R. 2001., Butterflies and moths. In *The changing wildlife of Great Britain and Ireland*, (ed. D.L. Hawksworth), pp.300-327. Taylor and Francis, London.
- Goodyear, L. and Middleton, A., 2003. The Hertfordshire Purple Emperor *Apatura iris*. The Hertfordshire Natural History Society.
- Haines-Young, R. H., Barr, C. J., Black, H. I. J., Briggs, D. J., Bunce, R. G. H., Clarke, R. T., Cooper, A., Dawson, F. H., Firbank, L. G., Fuller, R. M., Furse, M. T., Gillespie, M. K., Hill, R., Hornung, M., Howard, D. C., McCann, T., Morecroft, M. D., Petit, S., Sier, A. R. J., Smart, S. M., Smith, G. M., Stott, A. P., Stuart, R. C. and Watkins, J. W. 2000. Accounting for nature: assessing habitats in the UK countryside. DETR, London.
- Hardy, P. B. and Dennis, R. L. H. 1999. The impact of urban development on butterflies within a city region. *Biodiversity and Conservation* 8: 1261-1279.
- Heath, J., Pollard, E., and Thomas, J. A. 1984. *Atlas of butterflies in Britain and Ireland*. Viking, Harmondsworth.
- Hickling, R., Roy, D. B., Hill, J. K. and Thomas, C. D. 2005. A northward shift of range margins in British Odonata. *Global Change Biology* 11: 502-506.
- Hill, J. K., Thomas, C. D. and Huntley, B. 1999, Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society B* 266: 1197-1206.
- Hill, J. K., Collingham, Y. C., Thomas, C. D., Blakeley, D. S., Fox, R., Moss, D., and Huntley, B., 2001. Impacts of landscape structure on butterfly range expansion. *Ecology Letters* 4: 313-321.
- Hill, J. K., Thomas, C. D., Fox, R., Telfer, M. G., Willis, S. G., Asher, J. and Huntley, B., 2002. Responses of butterflies to 20th century climate warming: implications for future ranges. *Proceedings of the Royal Society B* 269: 2163-2171.
- Murray, J. B. and Wood, A., 2001. *Hertfordshire and Middlesex butterfly and moth report for 2000*. Hertfordshire and Middlesex Branch of Butterfly Conservation.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Laila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A. and Warren, M., 1999.
 Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579-583.

- Parmesan, C. and Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.
- Plant, C. W., 1987. The butterflies of the London area. London Natural History Society, London.
- Pollard, E. and Yates, T. J., 1993. *Monitoring butterflies for ecology and conservation*. Chapman & Hall, London.
- Pollard, E., Woiwod, I. P., Greatorex-Davies, J. N., Yates, T. J. and Welch, R. C., 1998. The spread of coarse grasses and changes in the numbers of Lepidoptera in a woodland nature reserve. *Biological Conservation* 84: 17-24.
- Preston, C. D., Pearman, D. A. and Dines, T. D., 2002. New atlas of the British and Irish flora. Oxford University Press, Oxford.
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. and Pounds, A. J., 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57-60.
- Sawford, B., 1987. The butterflies of Hertfordshire. Castlemead Publications, Ware.
- Thomas, C. D. and Lennon, J. J., (1999). Birds extend their ranges northwards. Nature 399: 213.
- Thomas, C. D., Bodsworth, E. J., Wilson, R. J., Simmons, A. D., Davies, Z. G., Musche, M. and Conradt, L., 2001. Ecological and evolutionary processes at expanding range margins. *Nature* 411: 577-581.
- Thomas, J. A., Rose, R. J., Clarke, R. T., Thomas, C. D. and Webb, N. R., 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology* 13 (Suppl.1): 55-64.
- Warren, M. S. 1992., The conservation of British butterflies. In *The ecology of butterflies in Britain*, (ed. R.L.H. Dennis), pp. 246–74. Oxford University Press, Oxford.
- Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M. G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S. G., Greatorex-Davies, J. N., Moss, D. and Thomas, C. D., 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**: 65-69.
- Williams, L. R., 2000. London butterfly monitoring report for 1999. London Naturalist 79: 87-102.
- -, 2001. London butterfly monitoring report for 2000. London Naturalist 80: 169-180.
- -, 2002. London butterfly monitoring report for 2001. London Naturalist 81: 113-121.
- Wood, B. C. and Pullin, A. S., 2002. Persistence of species in a fragmented urban landscape: the importance of dispersal ability and habitat availability for grassland butterflies. *Biodiversity and Conservation* 11: 1451-1468.